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DYNAMICAL EVOLUTION

A LECTURE DELIVERED AT THE
MARINE BIOLOGICAL LABORATORY AT WOOD'S HOLL
MASS., AUG., 1893

BY
JOHN A. RYDER

BOSTON
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FOURTH LECTURE.

DYNAMICS IN EVOLUTION.

JOHN A. RYDER.

THE statement that energy, in its kinetic and static forms, has been a factor in the production of the shapes of organisms, does not admit of question at the present time. In order that the data in support of this statement may be presented in their simplest forms, it is necessary to begin with the consideration of the physical causes of the configuration of some of the simplest unicellular organisms. In this way it will eventually be possible to pass from the consideration of the unicellular to that of the multicellular type, viewed from the same standpoint. It requires but little familiarity with the principles of physical science to discover that similar laws hold with respect to the behavior of fluid and semi-fluid bodies, notwithstanding the fact that we may have before us, in one case, a so-called "dead" fluid body, and in the other, a fluid or *fluent* "living" chemical compound or mixture of compounds. Though the one presents the phenomena of 'dead,' and the other of living, matter, both exhibit the similar and common properties of fluids, namely, those of surface-tension, viscosity and adhesion to the surfaces of other bodies, with which they are brought into contact. Under certain conditions, also, the semi-fluid cells of living bodies undergo reciprocal deformation or alteration in configuration, as a result of the interaction of the inherent forces above specified, in ways so precisely similar to those seen when a number of semi-fluid, or fluid dead masses, are juxtaposed or brought into contact, that the resemblances are seen to be due to the coöperation of closely similar, if not identical, forces and properties.

This remarkable resemblance of the physical behavior of semi-fluid living protoplasm to that of semi-fluid dead matter of certain kinds, such as the oils, has led me to apply the term *cytophysics* to the study of the physical properties of the substance of the cell. The convenient terms *cytostatics* and *cytokinetics* very naturally follow from a consideration of the contrasted states of rest and activity presented by the "living" cellular unit of organization. The cytostatic state will be one in which no visible physical activity, other than its secular metabolism, will characterize the cell, during which time, also, the parts of its substance will be in a condition of statical equilibrium in respect to each other, and the cell will, so long as this equilibrium lasts, maintain a constant configuration. The cytokinetic state, on the other hand, is one in which the visible or invisible parts of the cell are undergoing a displacement in respect to each other, as a consequence of which the cell as a whole will manifest changes of configuration.

Free and interfacial surface-tension is probably the most important factor in determining the shapes of cells, since there is associated with it, in multicellular organisms, a complicated series of definite and constant space relations and reciprocal interactions, as respects the cells of definite tissue-tracts, that grow out of the very conditions of combination of those tracts. Still more important, perhaps, are the incessant unequal disturbances of surface-tension, due to metabolic changes, at different points on the surfaces of cellular masses of plasma — a fact beautifully illustrated by the proteus animalcule, *Amœba proteus*. Differences of surface-tension are thus developed at different points and times coexistently and consecutively which lead to the assumption of the most diverse and inconstant shapes by the bodies of these lowly organisms. Such differences of surface-tension are, however, themselves caused by chemical and molecular transformations at definite, but previously unspecifiable, points at or near the surface of the mass of plasma. These processes are, therefore, ultimately to be associated with molecular or chemical transformations, the production of heat, the disintegration and integration of living matter.

But, it will be asked, what is surface-tension? If a drop of water falls through a vacuum, as long as it is falling in space it will present very nearly the form of a sphere. This is due to the fact that the very outermost layers of molecules which lie at insensible distances apart, attract each other with a force that is apparently very much greater than that developed by the action of gravitation. It results from this that the remaining molecules contained within this outer molecular film are held as within an elastic bag, the walls of which are of exactly the same strength at every point. This exactly equal strength and elasticity of the outer molecular film at every point on the surface also causes it to fall into a condition of spherical, statical equilibrium. This is true because the molecules at every point on the surface of the drop are of exactly the same size, therefore every one attracts its fellows that are in contact with it, with exactly the same force at every point on that surface. Now, let any change in the dimensions of these molecules occur at any point on the surface of such a fluid sphere, such as may be accomplished by chemical transformations and recombinations, such as oxidation or decomposition, and it must follow that the surface-tension or reciprocal pull of the molecules upon each other, adjacent to the point of such disturbance, must be increased or diminished. The inevitable result of this will be that the form of the drop must instantly change in order that a new condition of statical equilibrium may be attained. The surface of the drop is finite and returns in every direction upon itself since it is approximately spherical. Any deformation of the drop due to surface-tensional disturbances will therefore affect the shape and curvature of some or all of the surface of the drop so that its shape may become very irregular, provided its surface-tension be disturbed at a number of irregularly distributed points simultaneously; but, since the drop is a finite mass made up of solid particles moving freely among themselves, no matter how much the drop may be deformed or how irregular it may become, its most superficial layer of molecules will always form a closed surface. This fact is important, since, no matter how irregular in shape an *Amœba* may become, its outermost stratum of molecules always form a closed surface and a molecular envelope for the organism.

Since the molecules within a semi-fluid mass also move freely over one another there is friction developed between them. This friction is known as *viscosity*, and differs in fluids of differing densities and chemical compositions, just as, in fact, the surface-tension of a unit-surface, formed of different fluids, differs, owing to the differing dimensions and properties of the superficial layer of molecules of each fluid. The specific viscosities and surface-tensions manifested by any given fluid are therefore correlated, so that we may infer that these two properties of fluent living matter are also correlated. Since, again, living matter, as found in the cell, is not a homogeneous body or compound, it will be plain that the correlative disturbances in viscosity and surface-tension, due to the processes of metabolism and the associated interplay of osmotic changes, are so complex, when considered together with still other facts, that it will be difficult, if not impossible, in the present state of our knowledge, to trace *all* the steps of their interrelations and interdependences in any given case.

The recent progress in the study of the process of fertilization or conjugation shows that dynamical considerations must here also be taken into account. As is well known, the nucleus and archoplasm undergo alternate expansion and contraction in linear dimensions. The male and female pronuclei increase greatly in size during the phases just before conjugation. In the egg of *Ascaris*, for example, I have noticed that the pronuclei soon assume a globular form and rapidly grow into large spherical bodies by absorbing substance from the surrounding cytoplasm. This rapid growth and spherical form show that surface-tension is being disturbed uniformly over the whole surface of the nucleus, otherwise *its form could not remain spherical.* The remarkable growth of the rays of the asters has the same meaning and must also be interpreted, in part, as a physical process involving radial interdiffusion of heterogeneous molecules to and from the centrosomes into the nucleus and cytoplasm, consequent osmotic disturbances, metabolism and changes of surface-tension. The comparison of the astral figures, with their rays extending in every direction from the archoplasm, with the rays developed on the surface of a fluid when another fluid of definite properties is dropped upon the former, leading instantly to the production of a "cohesion figure" with rays extending out in every direction, is no mere analogy. In the case of the archoplasm, the rays with their lines of microsomes are probably the effects of diffusion of one kind of plasma, the archoplasm, through another, the cytoplasm, and is therefore not necessarily a phenomenon of contractility, but simply an interdiffusion of the unlike substances produced by the metabolism of growth, which tends to reëstablish statical equilibrium among the parts of the molecular system represented by the cell. This diffusion or osmotic redistribution is conditioned at every step by surface-tension in precisely the same way that the rays of many Heliozoa and Radiolarians are conditioned in water by states of unequal surface-tension at very close but nearly equal intervals over a spherical surface, so that a summation of these uniformly distributed and seemingly conflicting surface tensional forces does not interfere with the maintenance of the spherical figure by the body of the organism. The alternate inflation and collapse of the nucleus during fertilization, and growth during indirect cell-division, is a rhythmical process, and we may characterize it as the *diastole* and *systole* of the nucleus. The alternate extension and retraction of the rays of the archoplasm, as I have observed in the egg of *Ascaris*, is similarly an osmotic or metabolic diastole and systole of the radial figures formed by it, which is intimately associated with and absolutely conditioned by metabolism and osmosis, as the direct experimental researches of Prof. Jacques Loeb have rendered exceedingly probable. Unless the processes of karyokinesis are traced with the utmost caution in the light of dynamical and physiological considerations, there is great danger of our misinterpreting the facts and of assuming that certain of the phenomena guide and control others. It may indeed be possible that embryologists have been until now steadily confounding ontogenetic effects due to the physical processes of growth, as visualized in karyokinesis, with their causes. I anticipate that this remark will meet with a decided denial from most morphologists ; nevertheless it seems opportune to warn them that the problems they have before them can never be settled by purely morphological methods. If my contention that all ontogenetic problems must be approached by a most intimate combination of the methods of physical, physiological and morphological research is true, we are still far from having anywhere an ideal biological investigator. If it is true that we have been mistaking ontogenetic effects for ontogenetic causes, what a mass of speculation must probably be set aside. All that will remain, in fact, will be the many most valuable and beautiful results of observation made by our foremost morphologists.

It is not intended to thus minimize in any way the great and increasing value of morphological research ; what is really meant is, that there is danger of overrating the importance of morphology to the injury or exclusion of other disciplines of paramount importance. If, as we must suppose, there is such a perpetual flux and interflux of particles and molecules going on throughout the plasma of an egg, owing to the metabolism due to respiration and the consequent surface-tensional and osmotic disturbances during the earliest steps of development, it becomes inconceivable that any such morphologically conceived and entirely hypothetical bodies as "ids," "idants," "determinates," etc., can have a stable existence. The existence of such bodies as fixed entities of finite complexity is absolutely disproved by experiments of the most varied character in separating the first two or four blastomeres of the egg, since it is then found that, in each of these blastomeres, there still inheres the power to produce a perfect embryo. The hypothetical *ids*, *determinants*, *biophores*, *gemmules*, etc., must, therefore, be supposed to be capable of being halved and then quartered without destroying their potentialities. These and numerous other difficulties that cannot be discussed here, render it exceedingly probable that we must look in altogether another direction for an explanation of the processes of ontogeny, viz., to a study of the modes and conditions of the manifestations of the energies that constitute the "life" of the simplest organized forms.

In the very simplest unicellular organisms we have also unicellular molecular mechanisms of a most peculiar kind. The fearfully complex molecular structure of these mechanisms conditions their actions, their forms and powers, no less than does the nature of the watery media, in which these firstlings of life, as well as the germs of higher organisms, must in common develop. In the belief that the study of the "living" mechanism of some of the lowest types of organized existence, in relation to and as affected by their not-living surroundings, might throw some light upon the origin of their forms, the writer has here, in the main, taken up the problems thus raised as physical ones. In the belief, also, that these studies have not been entirely fruitless, the following evidence is offered.

An *Amœba proteus* may be compared to a smoke- or vortex-ring of particles that has been greatly modified, owing to the very complex interaction of disturbances of the surface-tension of its outer enveloping film of molecules, the viscosity of its own plasma, its gravity and power of adhesion to other bodies. If we conceive a smoke-ring to have become a viscous semifluid body with an outer film of molecules, and that this ring has contracted until the central opening in it has completely closed, we shall have a mechanism which may be compared in detail with an Amœba in motion, provided only that we modify it still further and in such ways as we are obliged to suppose that the combination of the four forces above specified coöperate in order to produce and maintain the form of an amœboid organism. Verworn[1] has already referred to the flux of the particles of the Amœba through itself, in discussing the general subject of contraction, but as he has not understood the complexity of the process, we need not here concern ourselves further than to say that he has failed to correctly interpret this vortical flux of amœboid organisms. There is, however, such a central flux of particles through the centre of the body of an amœboid, as any one can soon convince himself by carefully observing the behavior of a large living proteus animalcule. The chemical transformations that go on within the body of an amœboid, amongst its molecules, are responsible for disturbances of the surface-tension at one or more points over its surface. It is certain that the chemotropism, or affinity for oxygen of its surface molecules, as Verworn holds, is essential to this; but we must remember that in order to call forth local disturbances of surface-tension in this way, there must also be a locally exaggerated chemotropism, or affinity for oxygen, at some one point on the surface of the organism. This point has apparently not been made clear by Verworn, but it is essential to a clear understanding of the processes presently to be described. How the positions of such local disturbances of the chemical complexity of the surface-layer of molecules of an amœboid are determined, we do not know. That they are definitely determined, according to some definite law, we may be certain.

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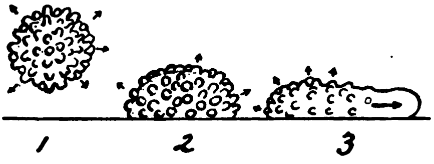
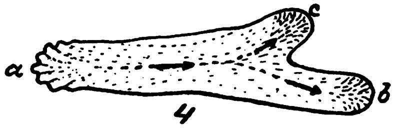
[1] Bewegung der lebendigen Substanz. Jena, 1892.

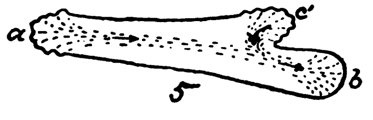
As every one knows who has ever watched a proteus animalcule under the microscope, the "anterior" pole of the creature, for the time being, is tensely filled with its own substance, so as to present a rounded, full "anterior" extremity while in motion. "Posteriorly," on the other hand, the creature is found to present a wrinkled, partially collapsed appearance. A study of the motions of the organism discloses the fact that its substance is flowing through itself. The central part of this current is moving most rapidly along the middle of the body, while toward the sides it is observed to become progressively slower until the outer layers of its substance, along the sides of the creature, are seen to come to rest. It thus results that the outer layers of molecules, along the sides, form a sort of shell or tunnel through which the central current flows. This flux, however, means that there must be a continual or fitful rupture of the "anterior" end of the organism in order to let some of itself escape out of itself in front, in order to let some of itself flow into itself behind, in order that some of itself may thus continuously flow through itself in order to make the progressive forward motion of itself possible. In this way the substance of the "posterior" part of the organism can be picked up and carried through the tunnel-like physical shell, formed of the outer layers of molecules of the organism.

and thus be transported forwards and poured out "anteriorly." It will readily be seen that, in order to do this, work must be performed, energy dissipated. This energy is dissipated in reëstablishing a dynamical balance between the parts of the dynamical system represented by the molecular aggregate that we behold in the body of the *Amœba*. We have here before us a finite molecular mechanism, or dynamical system, every part of the surface of which returns upon itself. Any disturbance of the equilibrium of the molecules at the surface of that system will provoke a deformation of the whole. If the disturbance is great enough at any one point, there will inevitably be developed a vortex-ring motion of the particles amongst themselves, due to the friction of the constituent molecules. If this vortical motion of the particles of an amœboid mass of "living" matter be due to a preponderating superficial disturbance of the equilibrium of the system at one point on the surface, that alone will suffice to determine the direction of the motion of the whole. For this reason the proteus animalcule has no fixed "head" or "tail" end. "Head" and "tail" seems to be entirely a matter of the combination of inner and outer conditions that determine the point on the surface of the organism, at which the maximum chemical and physical disturbance of surface-tension will occur. These are absolutely determined by the physical processes of the readjustment of the equilibrium of its molecules, in respect to outer conditions, during every consecutive moment of its motions. It is possible, in fact, to show that every change of the shape of this interesting organism is the result of energies inter-acting in a very complex way.

If an Amœba is allowed to fall through the water, its surface-tensions are apparently disturbed with great uniformity over its whole surface, and at nearly equal distances apart. It results from this that short, blunt pseudopodia are pushed out in every direction, as in Fig. 1 and it becomes nearly globular in outline. The moment, however, that the organism touches a plane surface, as in Fig. 2, it flattens out into the form of a biscuit-shaped mass. It now behaves like a mass of dough, and falls into a new condition of equilibrium, due to its own gravity, its viscosity, and the force with which the particles on its under side tend to adhere to the fixed solid surface upon which it rests. The upper part of the mass now falls into an equilibrium determined by the surface-tension of its superficial molecules and the viscosity or reciprocal friction of the latter upon each other. Gravity, viscosity, surface-tension, and adhesion are the four coöperating agents that now determine its figure. So long as it was floating or suspended in the water, the influence of gravity and adhesion operating in relation to a fixed surface were excluded. We thus see how completely this organism is the creature or subject of energy-conditions in this state.







In the next phase of its motions this is still further illustrated. In Figs. 1 and 2, short, blunt pseudopodia are being protruded in all directions; but in Fig. 3, the sequence of events changes, and the organism begins to take up its march by means of a vortical flux of its substance across the surface upon which it rests, and in the direction of the arrow. Surface-tensional disturbances of greater magnitude have evidently affected the right side of the mass, and one or more of the small original blunt pseudopodia at this point have been merged into a strong, single "anterior," pseudopodal current, in which a maximum flux of molecules is taking place in the direction of the motion of the whole organism. This maximum vortical flux of the material particles of the amœboid in this new direction will result in elongating the organism in th direction of the motion thus set up. The elongation of the organism is, therefore, due to the flow of its own particles amongst and through themselves. We are thus made aware ot the fact that this simplest organism is elongated in the direction of its own motions, as a consequence of the continuous readjustment of the internal equilibrium of its parts in respect to influences affecting it from without. The shape of this organism, at every instant of its motions, is, therefore, mechanically caused.

We may pursue our analyses still further. If we now look down upon such an amœboid organism from above, when moving upon a plane surface, as in Fig. 4, we find that it is not only elongated in the direction of its motion, but that its anterior end is tensely filled with substance; its outer layer of molecules at the "anterior" end is tensely stretched. At the tail end the organism is wrinkled or papillated; this wrinkled or papillated appearance of the posterior end of the organism is due to physical causes, as the following observation proves: In Fig. 4 there are two anterior pseudopodia, — *b* and *c*, — through which there are fluxes of particles in progress at about the same rate. The vortical current is seen to divide and to flow into both these pseudopodia, thus keeping the outer molecular film over both tense and rounded. Let, however, a disturbance of the surface-tension occur at the end of *b*, while at the end of *c′* this disturbance subsides, as in Fig. 5 and there will be a flux of particles out of *c′* — in the direction of the arrow — into *b*, and *c′* will lose its tense, full outline, and its surface will become wrinkled or papillated, just as appears at the "tail" end of the organism at *a*. In every detail of the morphology of this organism, we therefore discover that physical or "physiological" agencies are operative in determining its figure. We are, therefore, in a position to affirm, with positive certainty, that the morphology of this organism has little significance until its *actions* and their physical causes have been studied. This is only one of many reasons why the present speaker holds that all purely morphological work is one-sided, and incapable of dealing with the deeper problems of biology. In the same way, physiology alone is equally incapable of dealing with the great general problems in biology. Neither of the two disciplines *alone* can ever, by any stretch of imagination, command the power to produce *a theory of life.* Such an expectation is simply fatuous.

The many other dynamical phenomena, especially the singular manner in which the nucleus of an *Amœba proteus* is caused to oscillate back and forth within its body within certain limits, all take place in accord with the views above developed. For example, the curious lateral flow of the plasma of *Amœba proteus* when in a fully extended condition, along the sides of the body on either side of its posterior and middle thirds, may be explained by the physical tendency of this part of the organism to adhere to the substratum upon which it is moving. This lateral spreading does not take place at its "anterior" end because here the influx of molecules from behind is taking place so rapidly that this spreading due to adhesion has not yet had time to take place. This spreading due to adhesion causes the central current to be narrowed and elevated so that the discoidal nucleus is lifted and rolled along on its edge in this narrow elevated part of the body of the organism as if passing through a tunnel with its sides wider than its floor. Rolled along in this way through this narrow passage by the vortical current of plasma, the nucleus is finally arrested by contact of its edge with the molecular boundary wall of the organism, and is thus automatically kept from being bodily rolled to the outside of the plasma of the organism. Reaching a certain point at the "anterior" end of the mass of plasma, it also falls over on its side, wedged between the roof and floor of the mass of plasma of which it forms a part. It is thus prevented from passing out of the organism with the vortical current that must now flow past it and on forward to continually form anew the "anterior" end of this singular being that is thus continually turning itself inside outward in front and outside inward behind.

The manner in which the successive rents in the outer molecular skin of the organism are produced is such that a sudden rupture occurs through which a fresh outpour of substance happens over which a new molecular skin is instantly formed continuous with the ruptured edge of the old. These rents do not take place in relatively the same place in succession. For example, rents may occur in the outer film one after the other at points a little off of the extreme central point of the "anterior" end, and alternately a little to the right and left side of the latter. The vortical flux is thus thrown slightly aside alternately to the right and then to the left, then to the right, then to the left again, and so on, indefinitely. It thus results, however, that the summation of these alternating outbursts of substance become the components of the aggregate motion of the whole organism in one general direction.

If a rent occurs at one side of the organism, due to a disturbance of surface-tension at an anterior lateral point, a lateral flux of particles may thus be set up, as a result of which the entire contents of the organism may be sucked up "anteriorly" and "posteriorly" to the point where the new outflow has taken place. In other words, the "head" and "tail" ends of the organism may be thus caused to flow in opposite directions into the lateral outburst and the whole organism take a new direction of motion with all its parts oriented in respect thereto. *Amœba proteus*, therefore, cannot move except by developing a vortical flux of particles, and it therefore is a "living" vortex-ring of particles. These outbursts, in large individuals, occur successively at short intervals of time, so that the motion of the creature is fitful. In young proteus animalcules the bursting out or pouring forth of the plasma at the "anterior" end may be continuous, so that the motion is uniform and an ideally perfect type of the "living" vortex-ring of particles is realized.

Every pseudopodium is, however, so long as it is being protruded, a vortex-current in which the motion of the particles is swiftest at its center and at its tip, while at the sides the particles are quiescent and form a shell through which the central ones are moving. The pseudopodia, therefore, divide the vortex-current of particles into diverging currents, the summation of the motions of which may, when the organism is moving on a plane surface, become resolved mechanically into a single motion of translation in one direction.

When the organism is freely suspended in water it protrudes pseudopodia equally in every direction and assumes a globular figure, somewhat like a Heliozoan or Radiolarian, because its surface-tension is now being disturbed at nearly equally separated points over its whole surface. It therefore falls into a condition of spherical equilibrium, since the components of all the surface-tensions are resolved at the centre of the organism. The moment it touches a fixed surface, distortion of the formerly globular organism takes place under the influence of gravity and adhesion, and the vortical flux of particles that is now set up is different in nature from that which took place in every direction when it was in the suspended globular condition. There is at once a maximum flux of particles in the direction of the point at which the most active disturbance of surface-tension occurred, and the resulting current becomes very massive so that the whole contents of the organism, except the nucleus and water vacuole, flow forward as a massive pseudopod, that is somewhat flattened or depressed by the action of gravity and adhesion, but which is much larger than any of those produced while in the spherical condition. How little Verworn has appreciated and understood these complex processes may be judged by any one who has read his work on the motion of living substance. He has affirmed what does not exist in regard to small *Amœba proteus*, where the flux is continuous and where no retreat of particles to the nucleus, such as he postulates, can take place for hours together. In short, Verworn has totally failed to understand the real significance of these complex phenomena. Greef, also, has made assumptions with regard to amœboid motion, especially the existence of muscular fibrils, which by no stretch of the imagination can be conceived to hold of the proteus animalcule.

Verworn has also failed to understand the physical reasons why small blebs or pseudopodial warts were produced along the sides of a retracting pseudopod. He speaks of "stimulation"

(*Reiz*), a word which to me has a very indefinite meaning. The production of these blebs or incipient pseudopodia, which I have often observed, and in a great variety of forms, may be equally well explained by surface-tensional disturbance, the viscosity of the plasma, etc., and not necessarily as caused by a retreat of the substance toward the nucleus, as claimed by Verworn, in order to receive a reinforcement or accession of new nuclear molecules.

The differentiation of the substance of an amœboid, such as *A. proteus*, into an outer hyaline layer and a central or medullary part, — the so-called "endosarc" and "ectosarc," — is again a purely physical phenomenon. The surface-tensional forces *must* be exerted, for physical reasons, between molecules of approximately the same dimensions, otherwise there could be no tolerably coherent and stable outer stratum formed. In other words, the molecules of the outer layers are reciprocally attracted to each other with a greater force at insensible distances apart, than the larger and coarser particles are attracted by the small uniform molecules at the same intervals apart. The materials of an amœboid are thus dynamically sorted into two kinds, in virtue of their differences of attraction for one another. It thus comes about that "endosarc" and "ectosarc" are merely names for the results of a dynamical process that, so to speak, sorts the particles of a living amœboid into two kinds. The small surface-particles or molecules necessarily attract each other under such conditions of dynamical advantage over and above their attraction for the larger particles, that the latter are constantly driven inward and kept there for this reason.[1] In this case, again, a morphological fact is only understood when subjected to dynamical analysis.

In this way one might go on and subject every detail of the organization of an amœboid to physical scrutiny, and show that complex energy-combinations determined every detail of its structure. Not a single amœboid form that I have yet encountered has failed to disclose this mechanical and dynamical complex of agencies as factors competent to determine its figure at every instant of its existence. There may be those, however, who will find fault with my identification of the motions of an amœboid with that of a whirl- or vortex-ring of particles. It may be well, also, to explain here that this notion has nothing to do with the physical conception of Lord Kelvin respecting the existence of vortex atoms. The identification of amœboid motion with a vortex-ring of particles is perfect, provided certain reservations are made that grow out of the very nature of the conditions and nature of amœboid motion. In a typical smoke- or vortex-ring the impulse of rotation that impels all its particles is imparted from without; in the living vortex-ring secular changes in the nature of its constituent particles condition its motions and provoke them. And, while it is true that the energy that drives the living vortex-ring is primarily derived from without, it is not set free until the constituent particles have changed their dimensions, affinities, and reciprocal attractions within the ring, due to causes acting antecedently from without. The living vortex-ring is a constantly changing, closed, and regenerative dynamical system; the other is a dynamical system that derives all its energy from without in the form of a single impulse, and comes to rest after a time, owing to the friction of its superficial particles with their surroundings.

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[1] A geometrical diagram would be needed to make this statement perfectly clear.

It may be objected, also, that there is only a remote resemblance of a smoke-ring to that of the flux of living particles through an amœboid organism. This objection may be met by the statement, that not only do I suppose the living vortex-ring to be flattened by its gravity, but I also suppose it to have no central opening, and that the median longitudinal stream of particles represents the point where the opening would be in a smoke-ring — now a line in Amœba — along which the central "living" vortex current is flowing. I moreover suppose that the ring is greatly elongated, owing to the viscosity of its substance and the adhesion of the surface of the living amœboid to the substratum upon which it moves. I would not have any one suppose that I imagined that amœboids ever existed that had a central opening in them like a smoke-ring. I have only used this comparison because of the obvious identity of the living and dead vortices, when proper allowance is made for the physical conditions under which both subsist on account of the different nature of their constituent substances. The outer molecular shell, for example, of a living vortex-ring is fixed to its substratum, and is only involuted "posteriorly," and evoluted "anteriorly" as it moves over a fixed surface. These ideas once clearly grasped, will enable any one to see that, underlying the apparent unlikeness of the smoke-ring to a living amœboid vortex, there is in reality a fundamental similarity. The kind of "contractility" which is exhibited by an amœboid is thus also seen to be fundamentally different in nature from that presented by a muscle, in which contraction is conditioned by a vastly more complex structure.

When an Amœba passes into the resting stage its plasma is very apt to assume an almost perfectly globular form. Its pseudopodia are retracted; its surface becomes smooth, and the whole organism passes into the almost homogeneous, quiescent or lethargic condition of a ball of protoplasm that no longer manifests its characteristic types of motion and irritability, at least externally. Unequal surface-tensional disturbances no longer affect it; it is now under the domination of the same physical influences that determine the globular form of a sphere of oil in a mixture of alcohol and water of the same specific gravity as itself. Its cytoplasmic substance is nearly or quite homogeneous, and the excessively slow and torpid metabolic processes, within the protoplasmic mass of the Amœba, now secrete or pour out a cuticle or envelope over its surface and in which the organism is said to be "encysted." All of these processes are purely dynamical, just as were all of those associated with the motion of the organism. Not only are all of these processes dynamical, but all are also directly "adaptive," in virtue of the fact that the equilibria successively attained are merely a quantitative dynamical response from within a "living" molecular mechanism to a change in external energy-conditions. All "adaptation" is to be so interpreted, so that "natural selection" may be at last resolved into pure energy-factors, and thus brought into coördination with the rest of the forces of the cosmical universe. The mischievous metaphor, "natural selection," has blinded many naturalists to the real meaning of this expression.

In the same way we may discuss the characters of other amœboids. Each is found to have its own kind of plasma, that behaves differently in each species. Some move more rapidly than others, some have blunt, others long, slender or attenuated pseudopodia ; some may have bent pseudopodia, or have the axes of their straight pseudopodia normal to the surface of the spherical body of the organism ; others obey a different rule in this respect. In some the plasma is clear, in others more opaque ; in some the nucleus is globular, in others flattened. Thus one might go on and show that the different proportions and behaviors of the same parts, in different species, was evidence that totally different molecular mechanisms were simply making their necessarily different responses to the same environment, because of differences in the physical and chemical properties of their constituent plasma. Herein, probably, also lies the whole secret of the difference of power presented by the germs of different creatures. They develop as they do in the case of each species, because of their specific chemical constitutions, and not because there are a lot of "biophores," "gemmules," etc., "superintending" the business of development in a particular way during the evolution of the egg of each form. The preposterous assumption that enough energy can be squeezed into an egg potentially to carry the materials into place that are assimilated during development in order to build an elephant, for example, is worthy of mediæval philosophers, but not of those of the close of the nineteenth century. Every form of energy, including that of "life," is correlated, and is amenable to the same laws. Full knowledge of the mode of operation of the material energy-complexes that we call "living," will disclose the true theory of morphology and the true meaning of life as well.

These, here incompletely reported, observations make it tolerably clear that amœboid motion is worth studying, in order to get clear notions of how living motions and energies are operative in one of the simplest organisms known to the zoölogist.

They also make it very evident that observers have hitherto allowed purely morphological considerations to becloud their vision. In order to discover the meaning of the morphology of the simplest organisms, their actions must be subjected to the most searching analysis. These observations have proved that the functions of an organism are also functions of its form. It has been pretty clearly established, by what has been said above, that every action of the Amœba was followed by a morphological change. In the belief that this same thing holds good throughout the whole animal and vegetable world under most complexly interacting energy-conditions, I will predict what I believe will yet be possible, viz., the discovery of the true causes, in detail, of the forms of all organized existences. In order, however, to accomplish this end, the following will first have to happen, namely, an abandonment of all hitherto accepted hypotheses of inheritance, a new conception of the nature of life, new views of the nature of the process of natural selection, and, above all, the abandonment of all such conceptions as gemmules, biophores, pangenes, plastidules, plassomes, etc., and the admission that the phenomena of life are ultimately physical in their nature and are to be treated in detail as physical problems.

It is now my firm conviction, also, that experimental investigation in embryology will make no solid progress until the foregoing prepossessions are abandoned, or until the mischievous influence of such speculations and their kindred, as those regarding a "germ-plasm," etc., have been entirely eradicated from the minds of the present generation. In conclusion, let me remark that five sciences are indissolubly connected together in the study of the fundamental problems of life; these are: physics, chemistry, physiology, morphology, and psychology. When each of these sciences shall have been given its due weight and place in the conduct of the study of life-forms, we shall begin to know what the latter really mean, but not until then.

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